

# Phase Relationships Between Body Components of Odontocete Cetaceans in Relation to Stability and Propulsive Mechanisms

Frank E. Fish\*, John E. Peacock\*, and James Rohr\*\*

\* West Chester University, Department of Biology,  
West Chester, PA 19383 USA

E-mail: [ffish@wcupa.edu](mailto:ffish@wcupa.edu)  
\*\* Space and Naval Warfare Systems Center,  
San Diego, CA 92152-6004 USA

**Abstract-** For thunniform (lunate-tail) swimmers, propulsive movements were considered to be restricted to the caudal oscillating hydrofoil effectively minimizing drag. Previous reports on dolphin swimming have indicated substantial displacements of points along the body which oscillate in the vertical plane. To examine these vertical oscillations, video analysis was used to study the motions of the rostrum, pectoral flipper, caudal peduncle, and fluke tip for seven odontocete cetaceans. Animals swam over a range of speeds of 1.4 to 7.3 m/s. For each species, oscillatory frequency of the fluke tip increased linearly with swimming speed. Peak-to-peak amplitude remained constant with respect to swimming speed for all species. Mean peak-to-peak amplitude ranged from 0.02 to 0.06 body length at the rostrum and 0.17 to 0.25 body length at the fluke tip. Oscillations of the rostrum were nearly in phase with the fluke tip with phase differences of  $-9.41^\circ$  to  $32.95^\circ$ , respectively. Flipper oscillations trailed fluke oscillations by  $60.93^\circ$  to  $123.43^\circ$ . The lower range in amplitude at the rostrum compared to the fluke tip reflects increased resistance to vertical oscillation at the anterior end due to increased body stiffness and resistance on the flippers.

## I. INTRODUCTION

Analysis of propulsive systems in vertebrate animals generally has focused on the kinematics of the appendages for the generation of thrust. For animals swimming by movement of the pectoral and/or pelvic appendages, the body is rigid producing a minimum of drag. However, animals which swim by body and caudal fin propulsion are expected to experience increased drag over the body as a result of its movements. The anterior end of the body is displaced as a consequence of the movements of the tail, although recoil movements of the head are relatively small. For thunniform swimmers, such as tuna, lamnid sharks and cetaceans, propulsive movements were considered to be

restricted to the caudal oscillating hydrofoil (i.e., lunate tail) effectively minimizing drag [1, 2, 3].

Thunniform swimmers have a propulsive system that produces thrust with efficiencies higher than conventional propellers and thus, have become the focus of interest in the biomimetic development of underwater vehicles [4, 5, 6, 7]. Oscillatory motions of the head as a result of tail motions has been hypothesized as a mechanism to produce vorticity along the body that interacts with vorticity shed by the tail to enhance propeller efficiency and thrust production [4, 7]. However, oscillations of the head could potentially diminish the net thrust by increasing drag as the body deviates from a rigid body [1]. A further potential limitation to the application of oscillatory propulsion by organisms to marine technology is that the tolerances of engineered sensory systems may be unable to compensate for large displacements and accelerations at the anterior end. An understanding of the range of motion and mechanisms of control by thunniform swimmers, therefore, is required before implementation of oscillatory propulsion into engineered systems.

Unfortunately, there is a paucity of studies that have examined movements of the various body components of thunniform swimmers other than at the tail. Two reports on dolphin swimming have indicated substantial displacements of points along the body which oscillate in the vertical plane. Lang and Daybell [8] showed the outline of an accelerating dolphin (*Lagenorhynchus obliquidens*) with a transverse displacement at the rostrum of approximately 5% of body length. Outlines of a bottlenose dolphin (*Tursiops truncatus*) swimming at a routine speed of 2.63 m/s exhibited transverse excursions of 7.7% and 34.6% of body length at the rostrum and at the fluke tip, respectively [9].

This study makes a systematic comparison of the movements of various body parts with respect to each other for a variety of cetacean species. The analysis considered whether the transverse displacements of different body components is affected by body

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morphology and swimming speed. In addition, phase relationships between different body components were examined.

## II. MATERIALS AND METHODS

The swimming motions of seven species of trained odontocete whales were recorded at Sea World parks in Orlando, FL, San Antonio, TX, San Diego, CA and the National Aquarium in Baltimore, MD. The species examined included the false killer whale (*Pseudorca crassidens*), beluga whale (*Delphinapterus leucas*), pilot whale (*Globicephala melaena*), striped dolphin (*Lagenorhynchus obliquidens*), false killer whale (*Pseudorca crassidens*), spotted dolphin (*Stenella plagiodon*), bottlenose dolphin (*Tursiops truncatus*), and killer whale (*Orcinus orca*). Experiments were performed in large elliptical pools with maximum lengths of 27.4–48.8 m. The curved portions of each pool were constructed of glass panels. A water depth of 1.4–2.1 m was visible through the panels. Depth of the pools was 7.3–11.0 m and water temperatures ranged between 12 °C and 22°C. Whales swam routinely along the wall of the pool or under the direction of human trainers. All whales were trained to swim near the water surface. The speed of the animals varied in response to cues from trainers.

Morphological measurements were obtained from scaled photographs, including body length ( $L$ , m) as the linear distance from rostral tip to fluke notch, flipper length as the linear distance from anterior flipper insertion to flipper tip, fluke span as the linear distance between fluke tips, planar surface area of flukes, planar area of the flippers, and maximum body diameter.

The swimming motions were recorded with a Panasonic VHS camcorder (DV-510) at 60 Hz. Sequential positions of the rostrum, flipper tip, caudal peduncle, and fluke tips (Fig. 1) were digitized from individual fields of videotape with the Peak Motus video analysis system (Version 4.3.1) input from a Panasonic AG-73W video recorder. Kinematic data from film or videotape records included mean swimming velocity ( $U$ , m/s), stroke cycle frequency ( $f$ , Hz) and peak-to-peak amplitude ( $A$ , m) for each digitized point, and phase difference between the motion of the flukes and the motion of the other three body components. Peak-to-peak amplitude is the maximum vertical displacement. Due to size differences between species, comparisons were made on length-specific values as  $U/L$  and  $A/L$ . Phase differences in degrees were calculated as the time difference between the fluke tip and the other body point divided by the cycle period and multiplied by 360°. Negative values indicated cycle of the

body component trailed the cycle of fluke tip; whereas, positive values indicated the cycle of the body component led the fluke tip.

Statistical means were calculated for values that did not vary with  $L$  and  $UIL$ . Variation about means was expressed as  $\pm$  one standard deviation (SD).

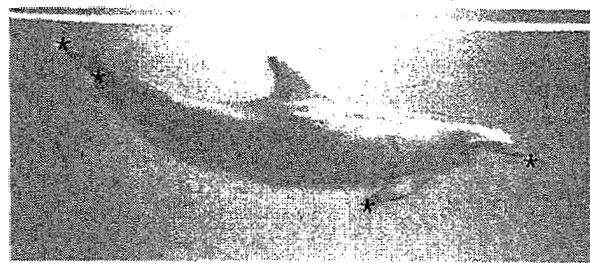


Fig. 1. Dolphin showing digitized points on rostrum, flipper, peduncle and flukes.

## III. RESULTS

The cetacean species examined varied in morphology related to body size. Body length among species varied 2.8-fold from 1.83 m (*Stenella*) to 5.16 m (*Orcinus*).  $FR$  varied from 4.66 (*Delphinapterus*) to 6.72 (*Pseudorca*). Flipper length, combined flipper area, fluke span, and fluke area increased with body length. Regardless of their functions for propulsion by the flukes and stability by the flippers, the planar areas of the appendages were similar.

A total of 143 swimming trials were analyzed. Video recordings showed that all the species swam steadily in a manner similar to previous descriptions of cetacean locomotion [8, 9, 10]. All body components measured moved along sinusoidal pathways (Fig. 2). The frequency of the propulsive cycle ( $f$ ) increased linearly with increasing length-specific velocity ( $U/L$ ) when all species were combined.

The vertical excursion,  $A$ , was greatest for the flukes, the peduncle, rostrum, and flipper, which showed the smallest oscillatory motions (Fig. 2).  $A$  was found to be independent of  $U$ .  $A$  for the flukes was shown to directly vary with  $L$ , whereas no significant increase in  $A$  was observed for the rostrum with increasing  $L$  (Fig. 3). Variation in mean  $A/L$  for the rostrum between species was small (Fig. 4), varying from  $0.02 \pm 0.01$  to  $0.06 \pm 0.02$ . For the fluke excursion, mean  $A/L$  varied from  $0.17 \pm 0.02$  to  $0.25 \pm 0.03$ . Both the fluke and rostrum mean  $A/L$  were found to be smallest for *Globicephala* and largest for *Stenella*.

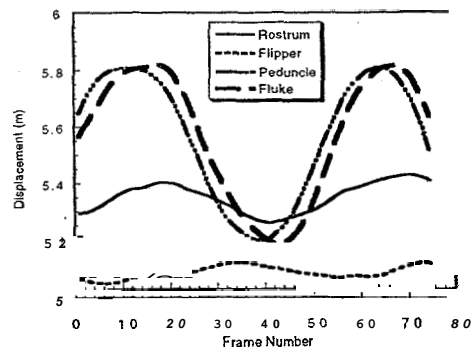


Fig. 2. Oscillations of body components for swimming *Tursiops*.

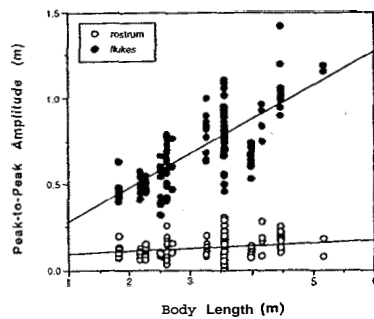


Fig. 3. Peak-to-peak amplitude ( $A$ ) plotted as a function of body length ( $L$ ).

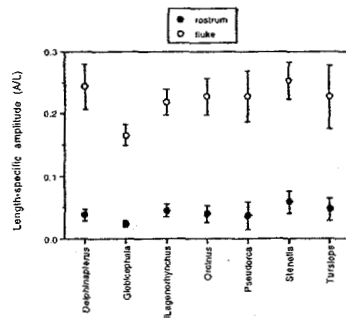


Fig. 4. Mean length-specific amplitude ( $A/L \pm SD$ ) for the rostrum and flukes for each species.

The phase difference between the fluke oscillation and those of the rostrum were consistently small for all species (Fig. 5). This indicated near synchrony between the rostrum and the flukes. Phase difference ranged from  $-9.41 \pm 13.83^\circ$  for *Lagenorhynchus* to  $32.95 \pm 21.30^\circ$  for *Delphinapterus*. With the exception of the negative mean values for *Lagenorhynchus* and *Tursiops*, the mean phase difference was positive for the cetaceans. This indicated that the motion of the rostrum led the fluke motion. In all

cases, the motion of the peduncle led the flukes by  $18.93 \pm 5.91^\circ$  to  $48.66 \pm 26.91^\circ$ ; whereas the flippers were out of phase by  $-60.93 \pm 24.75^\circ$  to  $-123.43 \pm 29.85^\circ$  following the flukes (Fig. 6). No relationship was found between phase relationship between the body components and  $U$ .

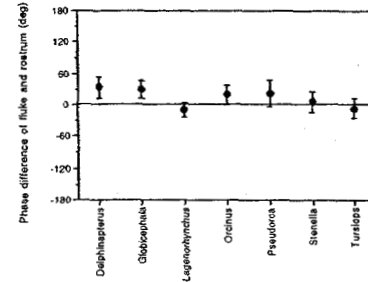


Fig. 5. Phase difference ( $\text{deg} \pm SD$ ) between flukes and rostrum for each species. Negative values indicate rostrum follows flukes; positive values indicate rostrum leads flukes.

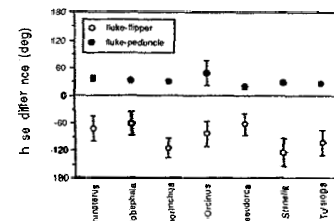


Fig. 6. Phase difference ( $\text{deg} \pm SD$ ) between flukes and flipper and peduncle. Flippers always followed flukes (negative values); peduncle always leads flukes (positive values).

#### IV. DISCUSSION

Propulsive oscillatory motions of the tail produce transverse forces that must be balanced at the anterior end of the animal. It is necessary to limit the transverse movements of the head to reduce drag, increase efficiency, and maintain stability. Large deviations at the anterior end will increase the added mass of the system as the water adjacent to the body is accelerated by its movements[11]. The drag is dependent on the added mass which is an indication of the kinetic energy dissipated in the water. In addition, transverse movements increase instability which potentially causes the animal to deviate from its chosen trajectory and increase its energy expenditure to maintain course.

Fish reduce the lateral displacement of the head by their kinematics and morphology. Recoil forces are balanced by throwing the body into at least one complete wavelength [2, 12]. As the wave travels posteriorly down the body, the opposing lateral forces are cancelled out. During fast-starts where trajectory is important, such as lunging by a predator toward prey, fish use a S-start [13]. The S-start bends the fish into a double flexure. S-starts avoid the recoil problem [14].

The use of multiple body flexures to reduce yawing is possible in elongate animals. Animals with short or inflexible bodies reduce recoil by changes in the distribution of projected area in the direction normal to flexure [1]. Recoil forces at the head can be resisted by increasing the area around the center of mass. This produces a large moment of inertia resisting recoil from the movement of the tail. Thunniform swimmers reduce the posterior area of the body by narrow necking. In narrow necking, the projected area decreases progressively from the center of mass to the caudal peduncle, with a rapid increase in the span of the caudal propulsor [1]. Furthermore, the peduncle is streamlined in its plane of oscillation. These modifications reduce the added mass effect posteriorly and corresponding recoil forces [2, 12].

For cetaceans, the low  $AIL$  (0.2-0.6) at the rostrum despite the relatively large  $A/L$  (0.17-0.25) at the flukes and phase relationship between both body components indicate control of pitching oscillations. The reduced area in the peduncle region would assist in minimizing recoil in the vertical plane [1]. Alternatively, the position of the flippers increases both the area and span of the body anterior of the center of mass. This increased area would increase the added mass and inertia at the anterior end of the animal effectively dampening recoil movements [2]. The large phase difference between the motions of the flippers and the flukes would generate vertical forces at the flippers which would counter the vertical forces produced by the flukes. Furthermore, increased stiffness of the anterior body due to skeletal mechanics limits pitching movements at the rostrum [15].

The resistance to pitching of the anterior body of cetaceans lowers the power requirements for swimming and increases stability. These are important requirements for cetaceans as fast-swimming aquatic predators. Stability is essential in the use of echolocation to target prey and the ability to rapidly pursue prey.

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